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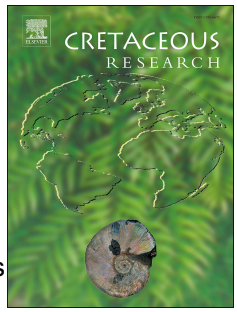

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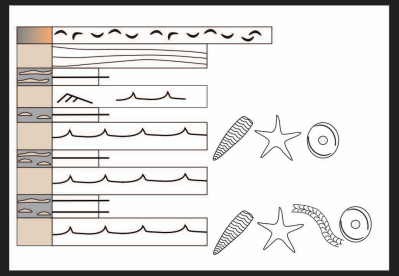
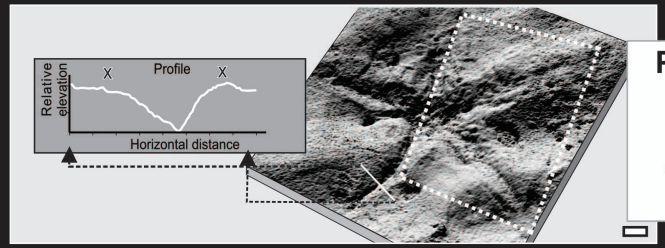
Lower Cretaceous, Patagonia



ASTERIACITES



Photogrammetric procedures are used for enhancement of features

BIVALVE TRACES

SECOND RECORD OF ASTEROIDS FROM THE LOWER CRETACEOUS OF SOUTH AMERICA

ICHNOTAXONOMIC DISCUSSION

ASTROPECTINIDS

PREDATOR PREY INTERACTION

Asteroid trace fossils from Lower Cretaceous shallow- to marginal-marine deposits in Patagonia

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Abstract

Most stellate trace fossils of the ichnogenus *Asteriacites* are attributed to asterozoan producers in general and the majority is the result of the work of ophiuroids. The fossil record of asterozoans

is scarce in South America, particularly for the Mesozoic. *Asteriacites* specimens found in shallow- to marginal-marine Lower Cretaceous (upper Hauterivian-lower Barremian) deposits in the Neuquén Basin (Patagonia, Argentina) exhibit sculpture and morphometry typical of asteroid producers. This is the second record of asteroids from the Lower Cretaceous of South America. The close association between these *Asteriacites* possibly produced by astropectinids and traces assignable to Siphonichnidae are suggestive of a predator-prey interaction, adding palaeoecological information for community-structure reconstruction of these deposits. For ichnotaxonomic evaluation, morphometric parameters of *Asteriacites* were elaborated using simple photogrammetric procedures applied on negative epirelief specimens and undertraces to define edges of the stellate trace fossils.

Keywords: *Asteriacites*; asteroids; palaeoecology; predator-prey interaction; ichnotaxonomy; morphometry.

1. Introduction

The ichnogenus *Asteriacites* von Schlotheim, 1820 includes stellate trace fossils (Seilacher, 1953; Häntzschel, 1970). Most records of *Asteriacites* are attributed to asterozoans as producers in general and the majority is the result of the work of ophiuroids (Mángano *et al.*, 1999, and references therein). Such trace fossils provide a valuable record of asterozoan activities (see recent review by Knaust and Neumann, 2016), because the producing organisms tend to disarticulate after death very rapidly (e.g., Villier et al., 2004). Especially, for South America, the asterozoan record is scarce for both body and trace fossils (e.g., Martin-Medrano and García-Barrera, 2013; Fernández et al., 2014; Martínez and del Río, 2015). So far, asterozoan trace

fossils are known from two units of the Neuquén Basin, the Jurassic Las Lajas Formation, where the presence of *Asteriacites* has only been mentioned (McIlroy et al., 2005), and the Cretaceous Mulichinco Formation where *Asteriacites lumbricalis* has been found, described and attributed to ophiuroids (Rodríguez et al., 2007; Fernández, 2013).

The new finds of *Asteriacites* in the shallow- to marginal-marine, upper Hauterivian-lower Barremian Agua de la Mula Member (Agrio Formation, Neuquén Basin, Patagonia), thus, provides new data to the asterozoan record in general and in particular to the community structure of these deposits. In addition, excellently preserved primary sedimentary structures help to decipher the environmental setting of the Agua de la Mula Member in more detail and the habitat of the *Asteriacites* producers in general. It is the purpose of this paper (i) to describe these specimens in detail, (ii) to evaluate their ichnotaxonomy, (iii) to outline their palaeoecological implications, and (iv) to refine the palaeobathymetric interpretation of the studied deposits.

2. Geological and palaeontological setting

The Neuquén Basin is located in west-central Argentina between 34° and 41°S (Fig. 1A). It represents an epicontinental basin in back-arc position to the Palaeo-Pacific–Andean subduction zone (e.g., Howell et al., 2005, Zapata and Folguera, 2005). It contains more than 7000 m thick marine and continental deposits being Late Triassic to Palaeogene in age (Vergani et al., 1995; Legarreta and Uliana, 1999). Most of the Jurassic and Early Cretaceous deposits formed in marine settings while temporarily enhanced subsidence and sea-level fluctuations accentuated the diverse, fossiliferous facies (Howell et al., 2005).

The Agua de la Mula Member (Leanza et al., 2001; Fig. 1B) of the Agrio Formation (Weaver, 1931) was studied in detail in the Neuquén Province. It is late Hauterivian to early Barremian in

age (Aguirre-Urreta et al., 2007, 2008, 2015; Aguirre-Urreta and Rawson, 2012). The depositional environment of the Agua de la Mula Member has mainly been interpreted as an open marine ramp (Spalletti et al., 2001a; Lazo et al., 2005; Ballent et al., 2006). However, marginal-marine intervals are recurrently present, particularly in the upper part of the unit (Pazos and Fernández, 2010; Fernández and Pazos, 2012, 2013; Pazos et al., 2012).

The Agua de la Mula Member was studied in detail at Bajada del Agrio, the type locality of the Agrio Formation, located between 38°25′S/70°00′W and 38°26′S/70°01′W (Figs. 1, 2). There, the entire unit is 470 m thick. At Bajada del Agrio, the upper part of the Agrio Formation is interpreted to have formed in shallow subtidal to proximal outer ramp sub-environments influenced by fair-weather and storm waves (e.g., Spalletti et al., 2001b).

The base of the logged section is located at GPS coordinates 38°25′23″S/70°00′42″W. The studied interval coincides with the uppermost part of the stratigraphic sequence Sq3 and the lowermost part of Sq4 of Guler et al. (2013). Within an inner ramp setting, it occupies a transitional position between basically shoreface deposits with intervals of upper shoreface sediments (Fernández et al., 2018) and shallow to marginal-marine sediments comprising tidal-flat deposits affected by enhanced and/or fluctuating salinity (Fernández and Pazos, 2012). Tides influenced the depositional area considerably as observed in other localities (Pazos et al., 2012) rather than storms as traditionally proposed (e.g., Spalletti et al., 2001b). The marginal-marine, tidally influenced deposits constitute the uppermost 63 m of the unit.

The Agua de la Mula Member contains varied and abundant macrofossils including bivalves, corals, ammonoids, gastropods, serpulids, sponges, echinoids, decapods, etc. (e.g., Cichowolski, 2003; Lazo et al., 2005, 2009; Rodríguez, 2007; Taylor et al., 2009; Aguirre-Urreta et al., 2011; Cataldo, 2013; Luci et al., 2013). Some groups are only known through their trace fossils (e.g. xiphosurids; Fernández and Pazos, 2013). So far, there is no record of asteroids in the unit.

3. Material and methods

The logged section begins 340 m above the transgressive base of the Agua de la Mula Member and ends in an oolitic-skeletal bar (Figs. 1B, 2). The latter represents the first level of the section analyzed in detail by Fernández and Pazos (2012). To provide a sedimentological and environmental framework, in total 73 m of over- and underlying strata were logged (Figs. 2, 3). While the Agua de la Mula Member is considered as homoclinal siliciclastic-carbonate ramp (e.g. Lazo et al., 2005; Guler et al., 2013), the depositional settings were accordingly classified based on the scheme of Burchette and Wright (1992).

Two specimens of stellate trace fossils were studied in detail (see field photographs on Figs. 3D, 4). Specimens A and B were found at 17.8 m and 18.6 m of the logged section, respectively (Fig. 2). Because of their occurrence in the field, the specimens were not recoverable. For enhancement of certain morphologic characteristics of the trace fossils, the images were processed with the photogrammetric software Agisoft PhotoScan Professional 1.0.4 build 1847 (64 bit), using standard methodology (e.g. Mallison and Wings, 2014). 3D meshes with texture overprint were used to enhance the imprints within each arm (Fig. 4E). 3D surfaces with shaded relief and contour lines as well as different profiles perpendicular to the arm axes were created using the software Golden Surfer (Fig. 4D). Given the scarcity of specimens the photogrammetric analyses were only accessory in the description as visual aid to better define the edge of the trace fossils (Fig. 4E). Morphometric analysis and ichnotaxonomic evaluation is based on Knaust and Neumann (2016).

4. Depositional setting

121

122 *Observations*. The studied section is characterized by coarsening- and shallowing-upward
123 packages (Figs. 2, 3). They range from 4–10 m in thickness (Figs. 2, 3A) and are considered as
124 parasequences in a sequence stratigraphic framework (e.g., Cichowolski et al., 2012). These
125 packages have thin bioclastic conglomerates at the base, indicating episodes of reduced
126 siliciclastic input. Above follow massive or laminated mudstones, thin lenticular and wavy
127 bedding, and finally fine-grained sandstones either massive or with wave-ripple lamination.
128 Within the sandstone interval, occasionally beds with current-ripple lamination, swaley cross-
129 stratification, and in some cases syndepositional deformation structures are present. At the top of
130 a package, sandstone bed surfaces may exhibit wrinkle structures (Fig. 3B), interference ripples
131 and parting lineation. Some ripples are flat-topped (Figs. 3E, F).
132 The *Asteriacites* specimens were found in two levels with dominant wave-ripple lamination
133 (Figs. 3C, D) in the package beginning at 14.5 m above the base of the logged section (Fig. 2).
134 Besides *Asteriacites*, other trace fossils occur in the logged section, such as cf. *Arenicolites*
135 Salter, 1857, *Bolonia lata* Meunier, 1886, *Chondrites* ?*intricatus* (Brongniart, 1823), *Gyrochorte*
136 *comosa* Heer, 1865, *Rhizocorallium* Zenker, 1836, *Siphonichnus* Stanistreet et al. 1980, tetrapod
137 swimming traces, arthropod trackways and invertebrate trails. *Chondrites*, *Gyrochorte* and
138 *Rhizocorallium* are also present in the overlying interval on top of the Agua de la Mula Member
139 (Fernández and Pazos, 2012).

140

141 *Interpretation*. The logged section is interpreted to represent marginal-marine deposits
142 accumulated in a proximal mid-ramp to inner ramp setting (cf. Burchette and Wright, 1992).
143 Wave ripples indicate a bathymetric range above the fair-weather wave base, while swaley cross-
144 stratification is a consequence of storm events in rather shallow water (e.g., Dumas and Arnott,

2006). The massive sandstone beds are either the result of intense indistinct bioturbation or rapid deposition from decelerating flows or wave pumping in association or not to soft-sediment deformation (e.g., Gingras et al., 2014; Liu et al., 2017). Intense bioturbation is the most likely process in intervals without syndepositional deformation. The heterolithic deposits are interpreted to have accumulated in a shallowing-upward setting characterized by mixed traction and suspension deposition forming first lenticular and then wavy bedding with oscillatory ripples that become replaced by current ripples (e.g., Reineck and Singh, 1980). The association of wrinkle structures with interference and flat-topped ripples suggests a marginal-marine setting. Interference ripples are typical of a very shallow depositional setting above the fair-weather wave base, while the flat-topped ripples reflect temporary subaerial exposure (e.g., Reineck and Singh, 1980). Although wrinkle structures occur within a wide palaeobathymetric range (e.g., Mata and Bottjer, 2009), they are most common in marginal-marine environments with shallow water experiencing intermittent exposure, such as tidal flats (e.g., Allen, 1984; Hagadorn and Bottjer, 1997). In addition, wrinkle structures have also been reported from a marine-marginal setting at the top of the Agua de la Mula Member exposed in another locality. There, clear evidence of tidal influence and temporary subaerial exposure have been observed (Fernández and Pazos, 2013). Indicators of subaerial exposure are present in three levels within the logged section, but not in the *Asteriacites*-bearing levels. Consequently, these intervals were formed under shallow-subtidal conditions above fair-weather wave base.

5. Ichnology

5.1. Ichnogenus Asteriacites *von Schlotheim, 1820*

Type ichnospecies. *Asteriacites lumbricalis* von Schlotheim, 1820; by subsequent designation of Seilacher (1953).

Diagnosis. Star-shaped, commonly pentamerous imprints and shallowly excavated pits with arms grading from a central area and continuously tapering distally (modified by Knaust and Neumann, 2016).

Remarks. The latest revision of *Asteriacites* applied hierarchically ordered ichnotaxobases: The overall appearance defines the ichnofamily Asteriacitidae, while the basic morphology differentiates *Asteriacites* from related ichnogenera (Knaust and Neumann, 2016). Sculpture was commonly applied as an ichnospecific ichnotaxobase (e.g., Seilacher, 1953; Crimes and Crossley, 1991), but due to its possible taphonomic bias it is now considered to be of subordinate value compared with other morphometric data such as the length/width ratio of the arms (Knaust and Neumann, 2016).

Description. Two specimens of pentamerous imprints preserved as negative epirelief (specimens A and B; Fig. 4). The sand laminae wherein the imprints are preserved are approximately 2−3 mm thick, while the whole bed in both cases is 3−4 cm thick. The arms are mostly straight except a slight curvature of one of them (Fig. 4D). The length from the central point to the tip of each individual arm is between 54.1 and 64.5 mm in specimen A (Fig. 4A), and 51.2 and 60.7 mm in specimen B (Fig. 4C). The largest width of the arms measured at their base varies slightly in each arm between 28.8 and 30 mm in specimen A and between 18.1 and 27.5 mm in specimen B. Some of the arms appear diffuse at their tips. The cross-sectional geometry of the arms is roughly V-shaped (Fig. 4D). Within each specimen, two areas are defined. The inner area close to the median line of an arm is 2−4.5 mm deep, sculptured, and rather regular in outline, while the outer area is less deep (1−2 mm), unornamented or finely striated, and less regular in outline (Fig. 4B). The imprints in both areas are oriented perpendicular to oblique to the arm axes.

5.2. Associated trace fossils

In the levels where the *Asteriacites* specimens occur, *Bolonia lata* and *Gyrochorte comosa* are common (Fig. 2). While *Gyrochorte comosa* is quite similar to those found further up in the section, as described by Fernández and Pazos (2012), *Bolonia lata* is reported for the first time from this unit. However, a detailed description of these trace fossils is beyond the scope of this study. Vertical burrows with a circular to oval cross-section, composed of a central core and surrounded by a concentric mantle, are assigned to the ichnogenus *Siphonichnus* (e.g., Knaust, 2015). These burrows are found closely associated with the *Asteriacites* traces (Figs. 4A, D, E). *Asteriacites* and the associated burrows do not cross-cut each other.

5.3. Ichnotaxonomic and preservational discussion

Three ichnospecies of *Asteriacites* are regarded as valid (Knaust and Neumann, 2016): *A. lumbricalis* von Schlotheim, 1820, *A. stelliformis* (Miller and Dyer, 1878), and *A. quinquefolius* (Quenstedt, 1876). *A. lumbricalis* is characterised by slender arms distinct from a central disc-shaped area (Knaust and Neumann, 2016), a feature not observed in the studied specimens. *A. stelliformis* presents arms having a length:width ratio >2, while in *A. quinquefolius* this ratio is <2 (Knaust and Neumann, 2016). The morphometric analysis of the studied specimens shows that for the arms the length:width ratio varies between 1.8 and 2.9. For 7 of the 10 arms the length:width ratio matches the value typical of *A. stelliformis* (>2). In specimen B the length:width ratio is >2 for every arm, but for specimen A three arms exhibit a length:width ratio <2 being characteristic for *A. quinquefolius*. In addition, the arm sculpture with respect to morphology and distribution of imprints resembles more that of the holotype of *A. quinquefolius* (Seilacher 1953, pl. 10, fig. 2), while the striae are not continuous as typical of *A. lumbricalis* (Seilacher 1953, 2007; Mángano et al., 1999; Knaust and Neumann, 2016; Ishida et al., 2017).

Based on the morphometric parameters of the current ichnospecies diagnoses, specimen A is assigned to *A. stelliformis*, while specimen B could be assigned to *A. stelliformis* or *A. quinquefolius*. However, because of the sculpture and while the majority of the arms shows a length:width ratio <2, an assignment to *A. quinquefolius* is suggested. It has been found in other *Asteriacites* that the width:length ratio differs between the arms of the same specimen, suggesting two different ichnospecific assignments (Singh et al., 2017).

The *Asteriacites* traces are preserved as negative epirelief in two separate sandstone beds showing dominance of wave-ripple lamination (Fig. 2). They are covered by thin mudstone layers. In neoichnological experiments with burrowing asteroids (astropectinids), rather indistinct depressions are formed on the sand surface, while the undertraces exhibit the structures more clearly (Seilacher, 1953). The outer arm area observed in the studied specimens (Fig. 4B) resembles that of the surface impression shown by Seilacher (1953, fig. 1a), while a rather sharp sculpture of the inner area resembles that of the undertrace. Furthermore, in aquarium well-preserved surface impressions show small mounds of sediment on both sides of the arms (e.g., Ishida et al., 2017). However, such structures are not present in the studied traces. They are, therefore, considered to represent an intermediate case between the two preservational types described by Seilacher (1953). Because the depth of the epirelief (3-5 mm) exceeds the thickness of individual sand laminae (1-2 mm) that formed during wave action, it is possible that the upper part (outer area) of the trace was affected by sand deposition during trace production and represents the original surface imprint, while the lower part (inner area) remained nearly unaffected or even could represent an undertrace. In the parts where the outer areas are unornamented, redeposition of sand by wave-pumping effects (Liu et al., 2017) and/or micro-avalanches due to originally unstable parts of the flanks cannot be ruled out as processes that "smoothed" the original profile and/or sculpture. In other cases, where specimens assignable to *A.*

241 *stelliformis* are attributed to asteroids (e.g., Ishida et al., 2013, fig. 3, specimen with arm
242 length:width ratio >2), preservation as shallow undertrace would explain nicely the high
243 length:width ratio of arm imprints, which would be lower for surface imprints of the same
244 specimen.
245
246 **6. Palaeoecological implications**
247
248 *Asteriacites* is attributed to both asteroids and ophiuroids as producers. Usually considered a
249 resting trace, it documents shallow burrowing. The movements of arms and tube feet might result
250 in arm impressions wider than the producing body parts, and distinctive sculpture inside the trace,
251 respectively (Seilacher, 1953, 2007). Asteroids usually have too broad arms to move the sediment
252 from one side of the arm to the other by a single tube foot. Seilacher (1953) described the
253 imprints of the tube feet of asteroids as discontinuous and irregular while ophiuroids produce
254 transverse and continuous striae. Recent neoichnological experiments focused on tube-feet
255 movement and the resultant striations ornamenting the traces of asteroids and ophiuroids (Ishida
256 et al., 2017).
257 For example, in the case of asteroids, in particular astropectinids, after forming a shallow burrow
258 and starting to move again in a particular direction, the striations differ within each arm
259 depression. The striations are wider and more regular in the half of the arm imprint opposite to
260 the direction of starfish movement, while they are fine and irregular in the other half. In the case
261 of ophiuroids, the striations are fine, regular and continuous from one side of the arm to the other.
262 In both cases, the striations are mostly perpendicular to the arm axis (Ishida et al., 2017).
263 The sculpture of the studied specimens resembles that resultant from the work of tube feet of
264 asteroids. Along each arm, areas with different ornamentation are found (see above). While the

265 striations are mostly perpendicular to the arm axis, they are not continuous (Fig. 4B). In
266 neoichnological experiments, tube-feet movement was observed on the surface of the substratum
267 as well as on the ventral and lateral sides of the glass beaker, and striations form at different
268 depths (Ishida et al., 2017). Thus, two areas having different striations are likely to be present in
269 shallow undertraces.
270 *A. stelliformis* can be produced by both ophiuroids and asteroids, but *A. quinquefolius* is
271 interpreted to be produced only by asteroids (Knaust and Neumann, 2016). In summary,
272 morphometric data and sculpture of the *Asteriacites* in particular the arm-width:arm-length ratio
273 point to asteroids as producers of the studied specimens. They were produced in very shallow
274 marine, subtidal environments as recorded in the *Asteriacites*-bearing levels.
275 So far there is only one record of asteroids from the Neuquén Basin from the Mulichinco
276 Formation and was assigned to *Tethyaster antares* Fernández et al., 2014, belonging to the family
277 Astropectinidae. Comparison of morphometric data between asteroid body fossils and trace
278 fossils has been used as tool for identification of possible producers (Ishida et al., 2013). The
279 arm-length:arm-width ratio of *T. antares* is between 2 and 2.26. When compared to the ratio
280 given for asterozoan trace fossils by Knaust and Neumann (2016) it mostly coincides with that
281 typical of *A. stelliformis* (>2), but it is also within the range of *A. quinquefolius* (<2). Therefore,
282 the only asteroid species known from the Lower Cretaceous, in particular early Valanginian of
283 the Neuquén Basin (Fernández et al., 2014), has a similar arm-length:arm-width ratio as the
284 studied asterozoan trace fossils found in the Agrio Formation (late Valanginian-early Barremian).
285 Extant astropectinids and paxillosidans in general are semi-infaunal, capable of self-burial in soft
286 sandy or muddy substrates and are common in marine settings from intertidal areas to the deep
287 sea (Heddle, 1967; Blake and Aronson, 1998; Jagt, 2000; Byrne and O'Hara, 2017). These
288 starfish are voracious predators that usually feed on other invertebrates like bivalves and worms.

289 They search for prey and shallowly dig into the substrate to get it while extruding the stomach
290 (Ortega et al., 2011 and references therein). Self-burial of asteroids evolved in relation to the
291 presence of fascioles that allow unobstructed water flow near the animals's body (Blake and
292 Aronson, 1998; Blake and Reid, 1998). These structures were already present in Valanginian
293 times (Fernández et al., 2014). Therefore, the producers of the studied *Asteriacites* were capable
294 to burrow. Consequently, the studied *Asteriacites* could be associated with different behaviour
295 types: (i) not-sustained resting (cubichnia) while shallowly burrowing; (ii) temporally prolonged
296 shallow burial, typical of a shallow semi-infaunal life style; (iii) active searching for prey within
297 the uppermost centimeters of the substrate; or (iv) combination of (i) to (iii).
298 Trace fossils of the ichnofamily Siphonichnidae are common in marginal-marine and shallow-
299 marine deposits. They are produced by infaunal bivalves adjusting their position within the
300 sediment (Knaust, 2015 and references therein). The presence of these trace fossils in close
301 association with *Asteriacites* are suggestive of a behaviour of the *Asteriacites* tracemaker to
302 burrow shallowly to locate prey. This adds information about the epifaunal-infaunal structure of
303 the studied deposits and possible ecological interactions. In the modern environments, some
304 starfish do not dig randomly, but accurately locate and capture infaunal bivalves; they produce a
305 pit often marked by furrows, which mirror the position of the arms (e.g., Smith, 1961; Doering,
306 1982). Although a possible predator-prey interaction is highly likely for trace fossils of asteroids
307 and infaunal bivalves, it has rarely been reported (Quenstedt, 1858; Seilacher, 1953; Mángano et
308 al., 1999). *Asteriacites* produced by asteroids have been usually linked to concealment and hiding
309 activities (e.g., Häntzschel, 1970; Seilacher, 2007). Deeper burrows attributed to asterozoan
310 activities are usually considered typical of dwelling, escaping or hunting purposes (Knaust and
311 Neumann, 2016). Nevertheless, surface trails and shallow burrows produced by modern sea stars
312 have been attributed to prey detection (Martin, 2013).

The latest neoichnological experiments provided additional insights into the morphology of shallow asteroid burrows and their sculpture (e.g., Ishida et al., 2017). Future neoichnological studies with asteroids and prey such as bivalves might help clarify the resultant morphology of the shallow burrows while the tracemaker is involved in prey detection and/or hunting, short-term vs. long-term burial, etc.

7. Fossil record of asteroids in South America

Fossil asteroids are scarce in South America. Body fossils are known from the Lower Devonian of Argentina and Brazil (Melo, 1988; Haude, 1995), the Upper Cretaceous of Brazil (Maury, 1930; de Castro Manso, 2006), and from Lower Cretaceous deposits in Argentina (Fernández et al., 2014). In Chile, Lower Cretaceous *Asteriacites* have been assigned to *A. lumbricalis* and ascribed to asteroids (Bell, 2004). So far it is the only South American record of trace fossils with asteroids as putative producers. Based on the figured material and the latest revision of the ichnogenus by Knaust and Neumann (2016), the specimens described by Bell (2004) should be classified as *A. stelliformis*. The arm length:width ratio ranges between 4.4 and 5.5 and hence, it is significantly larger than the established threshold value of 2. Furthermore, there is “no evidence of a central disc” (Bell, 2004, p. 56). Regarding the assignment of producers, when present the striae appear to be continuous from side to side, as typical of ophiuroid trace fossils. Therefore, this material needs to be revised, but it is currently unavailable (pers. comm. *Servicio Nacional de Geología y Minería*, Chile).

8. Conclusions

Stellate trace fossils are described in detail for the first time from the Lower Cretaceous Agrio Formation (Neuquén Basin, Patagonia). One specimen is assigned to *Asteriacites stelliformis*, and the other tentatively to *A. stelliformis* or *A. quinquefolius*, because three arms match the morphometric characteristics of the former ichnospecies and two arms those of the latter. However, the sculpture resembles that of *A. quinquefolius*. The sculpture and morphometric data imply asteroids as producers of these *Asteriacites*.

The clear definition of the boundary in asterozoan trace fossils, necessary to apply the morphometric parameters used in their ichnotaxonomic assignment, can be improved in negative epirelief specimens through simple photogrammetric procedures.

The *Asteriacites* represent the second record of asteroids in the Neuquén Basin, the first evidence of this group in the Agrio Formation, and one of the very few finds in South America at all. Until now, Astropectinidae is the only family of asteroids known from the Neuquén Basin and individuals belonging to it are considered as possible producers. The only astropectinid species described in the basin and the studied *Asteriacites* have a similar arm length:width ratio supporting the attribution to astropectinids. These animals are active predators capable of shallow burrowing. The close association of *Asteriacites* with bivalve traces assigned to Siphonichnidae suggests a predator-prey interaction between asteroids and bivalves in these deposits, adding information about the community structure.

The studied interval represents shallow-marine to marginal-marine deposits in a proximal mid-ramp and inner ramp setting. Interference and flat-topped ripples and wrinkle structures point to very shallow water depth even implying temporary subaerial exposure. Therefore, the depositional environment for this part of the Agrio Formation is shallower than previously assumed.

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597 pp.

598

599

600 **Figure captions**

601

602 **Fig. 1.** Neuquén Basin and stratigraphic column of the Agua de la Mula Member (Agrio
603 Formation). (A) Regional map of the Neuquén Basin in west-central Argentina showing outcrops
604 of the Agrio Formation (modified from Aguirre-Urreta et al., 2015). (B) Generalized stratigraphic
605 column of the Agua de la Mula Member. Note the studied interval, approximately 340 m above
606 the contact with the underlying Avilé Member (Agrio Formation). Modified from Aguirre-Urreta
607 et al. (2007).

608

609 **Fig. 2.** Logged section beginning 340 m above the base of the Agua de la Mula Member at
610 Bajada del Agrio and ending at an oolitic limestone level about 60 m below the base of the
611 Huitrin Fm. (see Fernández and Pazos, 2012). Depositional sequences taken from Guler et al.
612 (2013).

613

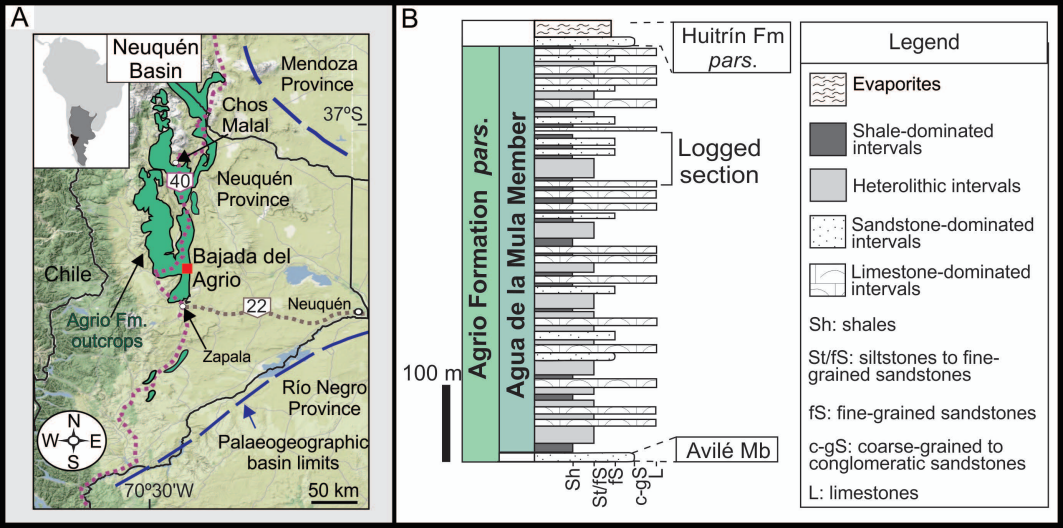
614 **Fig. 3**. Examples of sedimentary features of the logged section. (A) Example of coarsening- and
615 shallowing- upward packages. Graphic scale = 1 m. (B) Wrinkle structures. Graphic scale = 1
616 cm. (C) Wave ripples. Graphic scale = 6 cm. (D) *Asteriacites*, specimen A, and associated
617 ripples. Graphic scale = 2 cm. (E) and (F) Flat-topped ripples. Rock pick = 33 cm long. Coin =
618 2.1 cm in diameter.

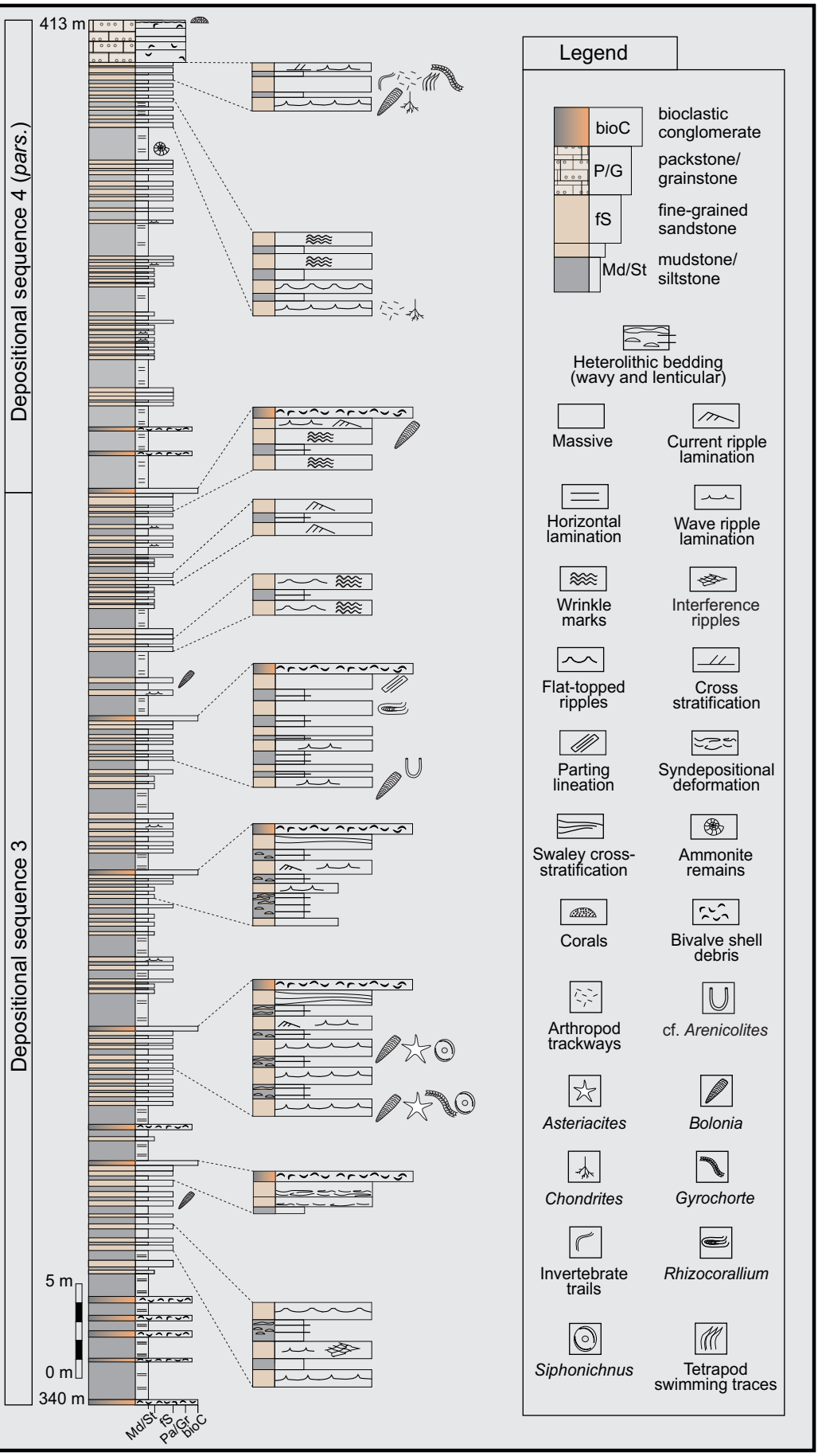
619

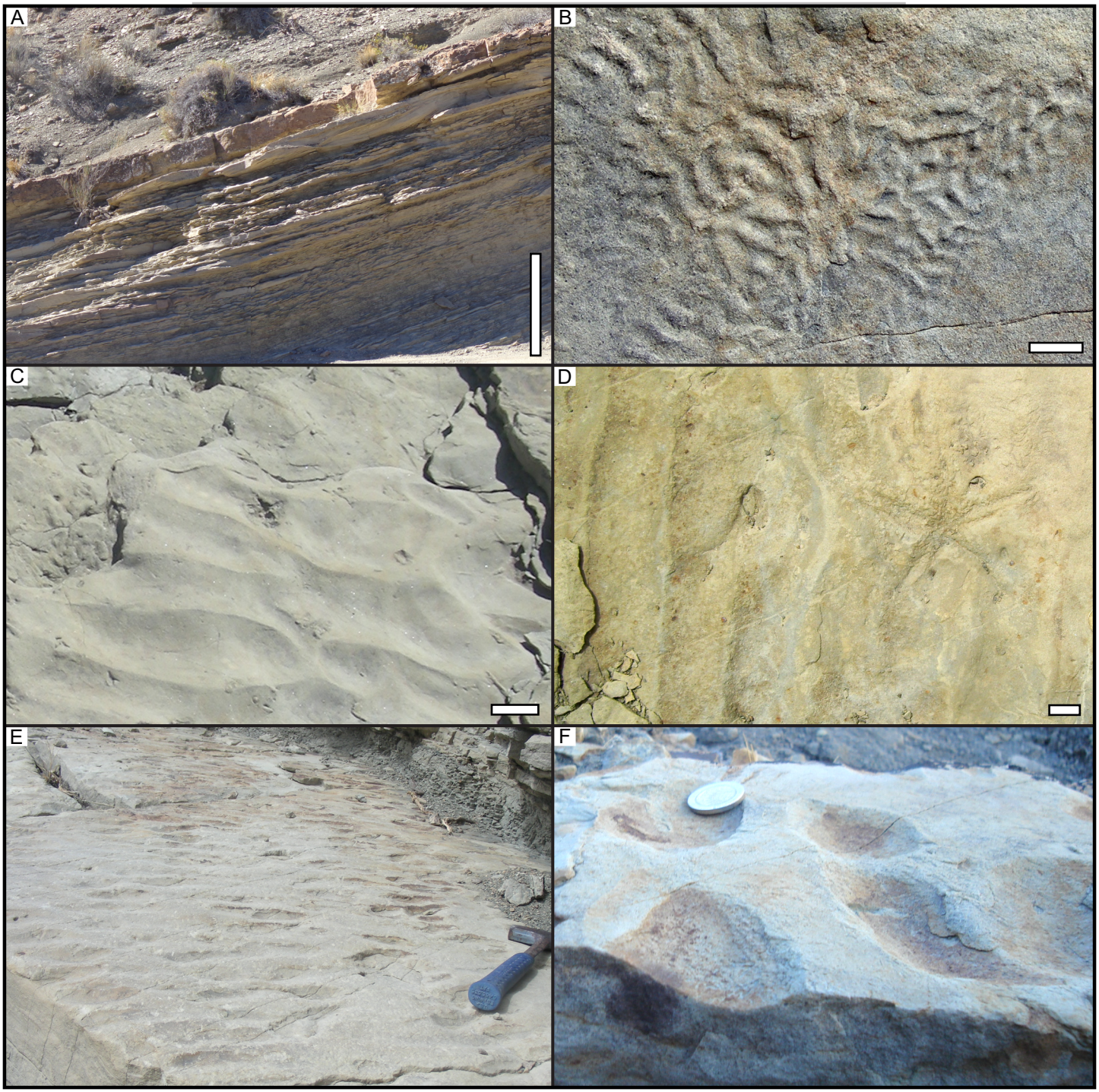
620 **Fig. 4**. Field photographs of *Asteriacites* specimens and examples of image analyses used as
621 visual aid for the description. Graphic scales = 1 cm in A, C and D, 2 mm in B and E. (A)
622 *Asteriacites*, specimen A. Si = trace fossil assignable to *Siphonichnus*. Si? = trace fossil assigned
623 to *Siphonichnus* with doubts. (B) Detail of the rectangle in A showing part of the arm imprint;
624 line drawing outlining striation features. WS = wide striations, RS = medium-sized striations, FS
625 = fine striations. The first two types of striae are restricted to the inner area of the arm imprint (as
626 defined in text), while fine striations are found in the outer area. (C) Specimen B. (D) Shaded
627 grey 3D photogrammetric model of specimen A and example of a relative morphometric profile
628 (location marked with white line) perpendicular to the arm axis. The Xs mark the areas of the
629 profile that helped defined the trace boundary. (E) Detail of the white rectangle marked in D
630 showing example of delimitation of the trace boundary.

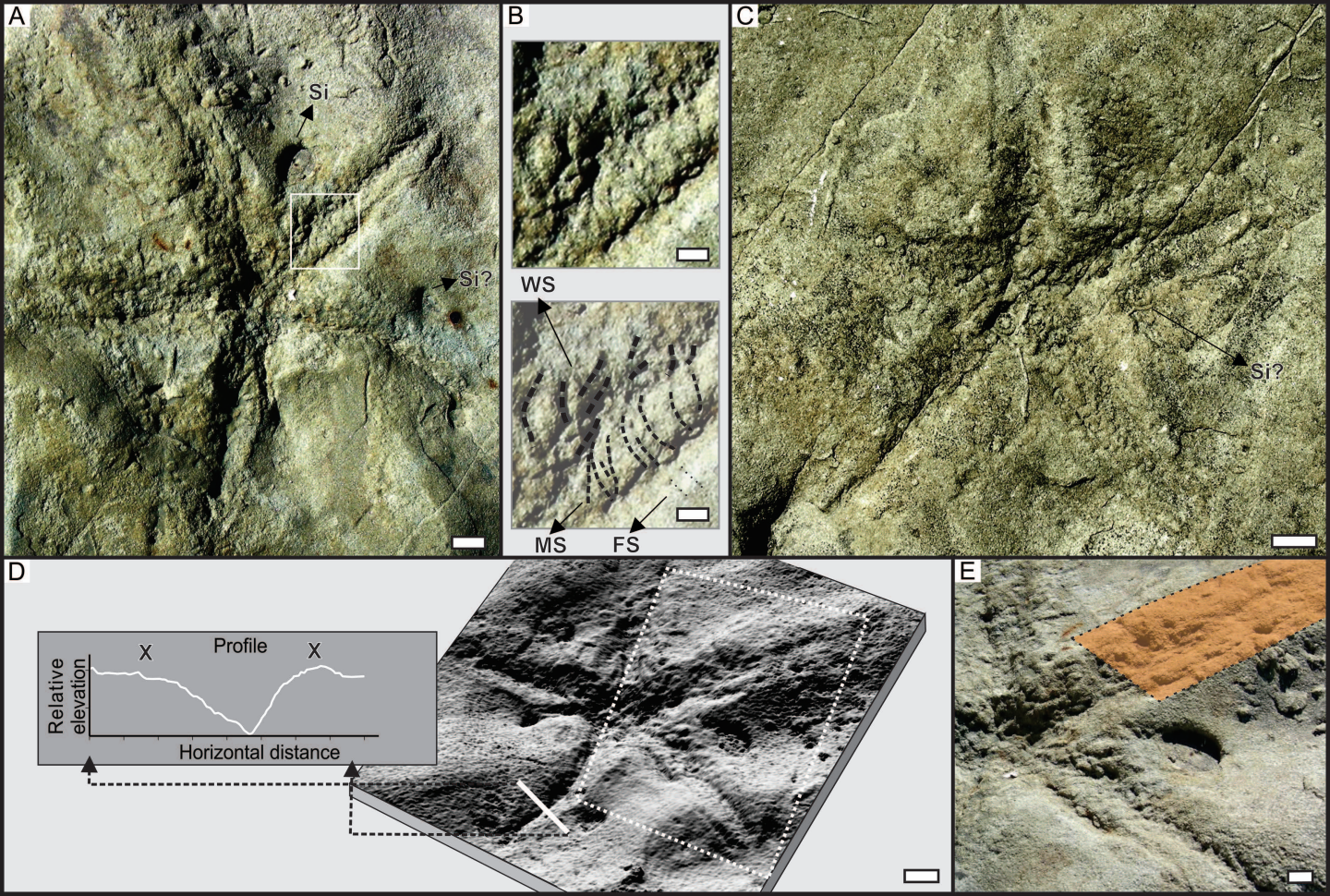
631

632


A
Neuquén Basin
Mendoza Province
Chos Malal
37°S
40
Neuquén Province
Bajada del Agrio
Chile
22
Neuquén
Agrio Fm. outcrops
Zapala
Río Negro Province
Palaeogeographic basin limits
N
W
E
S
70°30'W
50 km
B
Huitrín Fm pars.
Logged section
Agrio Formation pars.
Agua de la Mula Member
Avilé Mb
100 m
Sh
St/fS
fS
c-gS
L
Legend
Evaporites
Shale-dominated intervals
Heterolithic intervals
Sandstone-dominated intervals
Limestone-dominated intervals
Sh: shales
St/fS: siltstones to fine-grained sandstones
fS: fine-grained sandstones
c-gS: coarse-grained to conglomeratic sandstones
L: limestones


413 m
Depositional sequence 4 (pars.)
Depositional sequence 3
5 m
0 m
340 m
Md/St
fS
Pa/Gr
bioC
Legend
bioC
bioclastic conglomerate
P/G
packstone/ grainstone
fS
fine-grained sandstone
Md/St
mudstone/ siltstone
Heterolithic bedding (wavy and lenticular)
Massive
Current ripple lamination
Horizontal lamination
Wave ripple lamination
Wrinkle marks
Interference ripples
Flat-topped ripples
Cross stratification
Parting lineation
Syndepositional deformation
Swaley cross-stratification
Ammonite remains
Corals
Bivalve shell debris
Arthropod trackways
cf. Arenicolites
Asteriacites
Bolonia
Chondrites
Gyrochorte
Invertebrate trails
Rhizocorallium
Siphonichnus
Tetrapod swimming traces


A
B
C
D
E
F


A
Si
Si?
B
WS
MS
FS
C
Si?
D
Profile
X
X
Relative elevation
Horizontal distance
E

Highlights

Second record of asteroids from the Lower Cretaceous of South America

Rare example of asteroid predator-bivalve prey interaction in the fossil record

Photogrammetric procedures used for enhancement of features

Asteriacites attributed to astropectinids and discussion of ichnotaxonomic problems

New paleoecological and paleoenvironmental information for the *Asteriacite*s-bearing unit